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RESEARCH PAPER

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Lake expansion elevates equilibrium diversity via increasing colonization

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Abstract

Aim: Rates of colonization, speciation and extinction determine species richness and endemism in insular systems. The general dynamic model of island biogeography (GDM) predicts that speciation and extinction rates depend on island area and elevation via their control on ecological limits to diversification and therefore covary with an island's geological history. Additionally, the colonization rate may increase with area and elevation through the 'target effect', which can be mediated by reduced 'environmental filtering'. Here we test whether the area and depth expansion of an island-like ecosystem, a lake, caused a shift in diversity dynamics.

Location: Lake Biwa, Japan, whose geological history and biota are well documented.

Taxon: Fishes.

Methods: We extended the phylogenetic island biogeography framework DAISIE (Dynamic Assembly of Island biota through Speciation, Immigration and Extinction) to accommodate time-shifts in macroevolutionary rates and in carrying capacity. Using phylogenetic information on colonization and speciation times for the complete Lake Biwa fish community (70 taxa), we tested for a shift in macroevolutionary assembly rates and reconstructed the temporal diversity trajectory in the lake. We assessed the power to identify a shift through a wide range of scenarios and benchmarked against simulated fossil records.

Results: We detected an increase in colonization rate of fishes at 0.2 million years ago (Ma), with limited support for the existence of ecological limits. The reconstructed diversity trajectory was close to a source-sink equilibrium diversity prior to the shift and remained well below a new shift-driven elevated equilibrium thereafter. We found sufficient power to identify an increase in colonization rate up to 1.5 Ma, whereas extinction concealed the signal of earlier shifts.

Main conclusions: The fish diversity dynamics of Lake Biwa show a response to changes in area and depth and phylogenies carry a signature of these changes. The detected increase in colonization rate following Lake Biwa's expansion, elevating the fish diversity, is unlikely due to a predicted increase in ecological limits feeding back on colonization rate. We therefore call for (additional) explanations: the target effect,

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whereby larger islands attract more species, and reduced environmental filtering due to higher habitat diversity associated with increased lake area/depth.

KEYWORDS

colonization, DAISIE, diversity dependence, fishes, general dynamic model of island biogeography, Lake Biwa, source-sink equilibrium

1 | INTRODUCTION

Rates of colonization, speciation and extinction ultimately determine species richness, endemism and their trajectories through time in insular systems such as oceanic islands, mountain tops (sky islands) or lakes. In their equilibrium theory of island biogeography, MacArthur and Wilson (1963, 1967) proposed that islands tend towards a dynamic equilibrium, at which point rates of species gain via colonization (and in-situ speciation; Warren et al., 2015) equal the rate of species loss via extinction. This classic equilibrium view was later updated in the general dynamic model of island biogeography (GDM; Whittaker, Triantis, & Ladle, 2008). The GDM acknowledges that island features such as area, elevation and topographic complexity change throughout the life cycle of an island, and hypothesizes that these ontogenetic changes have an effect on rates of species assembly, leading to diversity dynamics characterized by an ever-shifting, often unattained equilibrium (Warren et al., 2015).

In this dynamic setting, there are different ways in which an equilibrium diversity (ephemeral or not) can theoretically be achieved. One is due to the presence of diversity dependence in rates of community assembly so that islands or clades have a carrying capacity that determines an ecological limit to species diversity (MacArthur & Wilson, 1963; Schoener, 2010). A different form of equilibrium is diversity-independent, and can be attained in the case that rates of extinction exceed rates of in-situ cladogenetic speciation—a source-sink equilibrium (Valente, Etienne, & Dávalos, 2017; Valente, Illera, et al., 2017). In both types of equilibria—diversity-dependent or source-sink—the level of equilibrium diversity can be affected by island geomorphological change.

The GDM proposed an effect of island area and elevation on the carrying capacity, which, in turn, shapes the strength of diversity-dependent rates of colonization and diversification (speciation minus extinction). Simulation experiments have supported this causal mechanism (Borregaard, Matthews, & Whittaker, 2016; Cabral, Wiegand, & Kreft, 2019; Valente, Etienne, & Phillimore, 2014), while empirical studies provided additional evidence by demonstrating the characteristic hump-shaped relationship of species richness and endemism with age and area of an island (Borges & Hortal, 2009; Whittaker et al., 2008), finding a persistent imprint of past archipelagic configuration on biodiversity (Norder et al., 2019) and by showing how speciation rates of insular taxa depend on their area or on a changing carrying capacity (Matos-Maraví et al., 2014; Rabosky & Glor, 2010). The level of equilibrium diversity resulting from source-sink dynamics (i.e. diversity-independent) may also vary

over the life cycle of an insular system upon changes in geomorphology and isolation. In both equilibrium cases, larger and higher islands are generally assumed to harbour larger population sizes. This reduces extinction risk (Rosindell & Phillimore, 2011) while allowing for higher opportunities for in-situ cladogenetic speciation (Losos & Schluter, 2000). Moreover, increasing island isolation has a negative effect on colonization rates and a positive effect on the number of species originated via in-situ cladogenesis and island-mainland differentiation ('anagenesis'; Valente et al., 2020).

A much less-explored explanation for the influence of island geomorphology on diversity is through a direct effect of area on rates of colonization. The 'target effect' (Gilpin & Diamond, 1976; Schoener, 1988) relates island colonization to its area—with larger islands being more frequently colonised than equally isolated smaller islands. While the original definition of the target effect relates to area, this effect can equally be translated to island elevation, with more highly elevated islands potentially being more frequently successfully colonised than islands with low elevation. An effect of area and elevation on colonization may also be due to a reduction in environmental filtering associated with increased habitat diversity in larger and higher islands (Cabral, Whittaker, Wiegand, & Kreft, 2019). However, these mechanisms remain empirically and theoretically understudied at evolutionary time-scales (Leidinger & Cabral, 2017; Wu & Vankat, 1991).

The precise way in which community assembly rates are modified as a result of island ontogeny remains unresolved. Addressing this topic requires a statistical method that includes all key parameters of island biogeography: colonization, speciation and extinction rates for entire island faunas, including their potential diversity dependence and, crucially, their change with island ontogeny. The Dynamic Assembly of Islands through Speciation, Immigration and Extinction model (DAISIE; Valente, Phillimore, & Etienne, 2015) is a phylogenetic diversification framework that allows estimating the rates of all these processes from phylogenetic data of insular communities, but so far assumes no time dependence in these rates. In this study, we extend the DAISIE model to estimate temporal shifts in rates of speciation, extinction or colonization. The extended version of DAISIE we present allows us to explore the effect of island geomorphological change on diversity dynamics. However, we note that geomorphological change does not serve as a direct causal predictor for the parameters in the DAISIE model: any inferred change in the rates can have a different origin.

Testing the consequences of insular ontogeny on evolutionary rates is best achieved using an insular ecosystem characterized by



(a) high species richness, because more data are needed to estimate up to twice the number of model parameters than the standard DAISIE model (i.e. rates before and after the shift) and (b) a medium level isolation, because such insular ecosystems are suggested to respond to alterations in area in a more pronounced way (Borregaard et al., 2016; Cabral, Whittaker, et al., 2019). Lake Biwa (Figure 1), located in the central Honshu Island of Japan, fulfils these criteria. It hosts 70 native fish species and subspecies, including 17 endemics (Figure 1a; Okuda, Watanabe, Fukumori, Nakano, & Nakazawa, 2014). The high proportion of non-endemics (76%) and the higher number of endemics presumably evolved through anagenesis (14) than through intralacustrine cladogenesis (3) suggest relatively low isolation of Lake Biwa, which may have been even lower due to the interconnection of drainage basins during glacial periods with low sea levels (Dias et al., 2014). Through its paleolimnological and geological history, Lake Biwa underwent changes in area and depth that were mainly driven by tectonic activity and monsoon climate (Iwamoto & Inouchi, 2007; Takemura, 1990). It originated as a shallow subtropical

lake 6–4 Ma and relocated about 40 km northwards through a series of paleo-lakes (Okuda et al., 2014; Takemura, 1990). Importantly, approximately 0.4 Ma, the final stage of geomorphological lake evolution featured the formation of the large northern deep basin of modern Lake Biwa (Figure 1b).

Recent studies attributed the increases in net diversification and population growth of several Lake Biwa taxa to the recent expansion of the lake (Miura, Urabe, Nishimura, Nakai, & Chiba, 2019; Tabata, Kakioka, Tominaga, Komiya, & Watanabe, 2016). Here, we complement these findings by investigating how the lake's expansion could have affected insular assembly processes and how this affected the diversity trajectory of its fish community. To examine the consequences of changing area and depth during the geological evolution of ancient Lake Biwa on evolutionary rates and richness trajectories, we apply our new extension of the DAISIE model that allows for rate shifts following lake expansion to a phylogenetic dataset accounting for all native Lake Biwa fish species. We explicitly test (a) whether colonization and diversification rates changed through time and

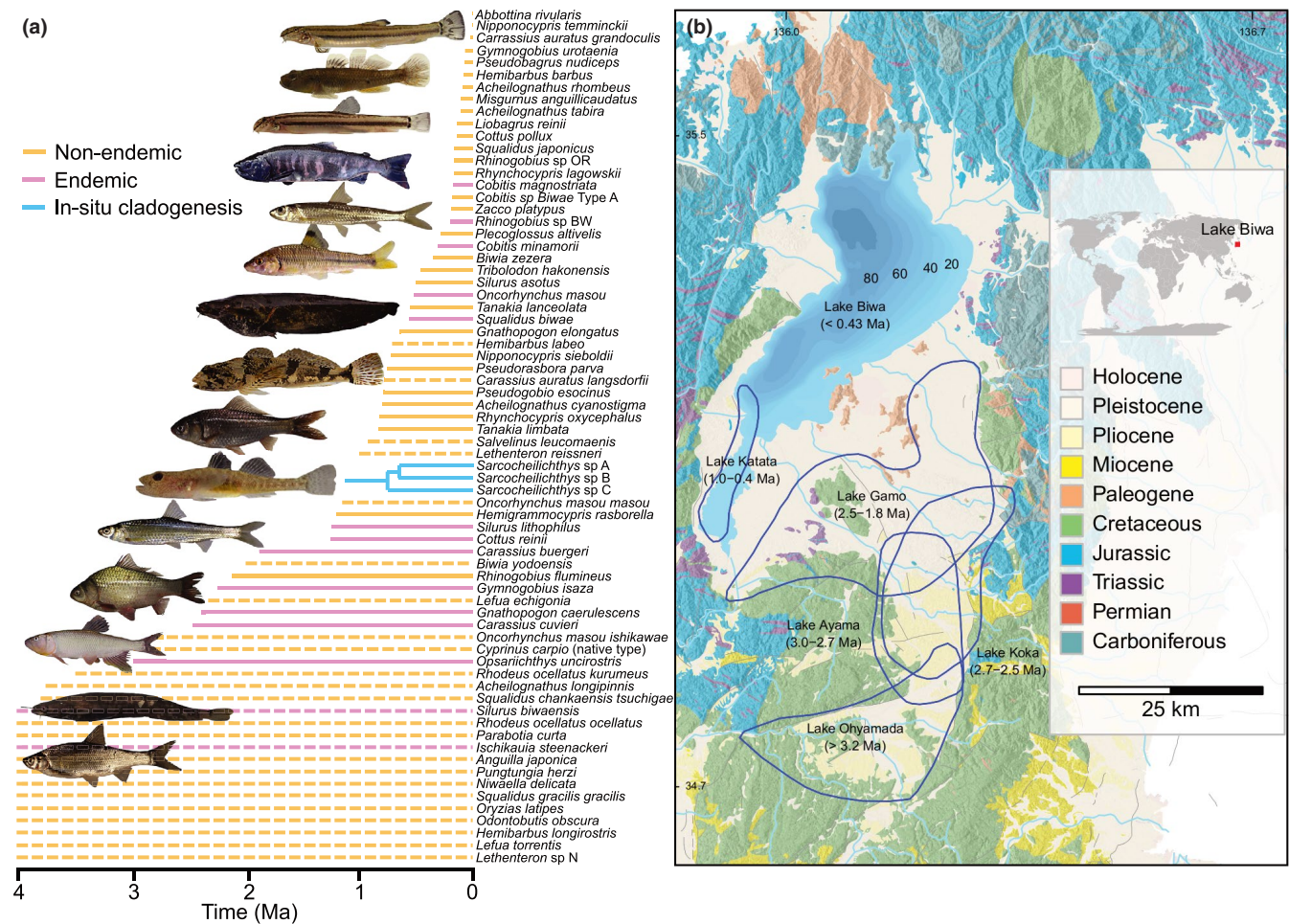


FIGURE 1 Colonization times of fishes of Lake Biwa (Japan) and its limnological changes over time. (a) Inferred times of colonization and in-situ cladogenesis. Dashed lines indicate taxa for which only an upper bound for the colonization time is known. Images of endemic taxa are displayed in order of their colonization times (pink and blue lines). Photographs were published by Tabata et al. (2016) under Creative Commons Attribution License. (b) Changes in location (northward movement) and size of Lake Biwa over time. Lake extents were redrawn from Okuda et al. (2014), geological information obtained from the Geological Survey of Japan (GSJ) web page and time-scale colour coded according to The Geological Society of America. Map projection: UTM 53N [Colour figure can be viewed at wileyonlinelibrary.com]

(b) whether these rates are subject to a reduced diversity-dependent regulation through an increase in carrying capacity. This enables us to test the prediction that evolutionary rates depend on insular ontogeny and provides insights into how the mechanisms underlying richness and endemism may unfold over time in a colonization-dominated weakly isolated insular ecosystem.

2 | MATERIALS AND METHODS

2.1 | Colonization and speciation times

We compiled phylogenetic colonization and speciation times for 68 of the 70 native fish species and subspecies of Lake Biwa from the literature (Table S1 and a list of the data sources is found in Appendix 1). The two species with missing phylogenetic data are the non-endemic species *Lethenteron* sp. (awaiting formal scientific description Okuda et al., 2014) and *Lefua torrentis*. Moreover, for the endemics *Silurus biwaensis* and *Ischikauia steenackeri* a phylogenetic age much older than Lake Biwa was retrieved in phylogenetic analyses (Tabata et al., 2016). The age of Lake Biwa was assigned as the maximum time of colonization of these four species, using the DAISIE option of 'Non_endemic_MaxAge' and 'Endemic_MaxAge', respectively. This integrates through all possible colonization times between a given time (in this case the age of the lake) and the present. We also used 'Non_endemic_MaxAge' status for all other non-endemic species in the dataset where the published available age was that of the split with its sister species instead of the split with conspecific non-Biwa individuals—that is, the age of the split was used as a maximum colonization time.

2.2 | Extending DAISIE to include temporal rate-shifts

DAISIE (Valente et al., 2015) is a dynamic stochastic model of island biogeography that provides the likelihood for the observed colonization and speciation times of an island community under a set of parameters for (a) colonising the system from the source pool at a per mainland-lineage rate γ , (b) extinction rate μ (like all following rates in units of per island-lineage), (c) anagenetic speciation rate λ^a , (d) cladogenetic speciation rate λ^c and (e) a carrying capacity K' that decreases colonization and cladogenetic speciation rate with increasing diversity of the colonising lineage. The original DAISIE model assumes that colonization, speciation and extinction rates are constant through time (except under the diversity-dependent version, where rates of speciation and colonization decline with increasing diversity).

We modified the general DAISIE model by allowing all parameters (or a subset) to shift in value at a particular moment in time. This was implemented by solving the system of differential equations for the DAISIE likelihood with the first set of model parameters until the shift, and with the second set with new rates until the

present. We implemented this extended model as function DAISIE_SR_ML_CS in the package 'DAISIE' 2.0 (Etienne, Valente, Phillimore, & Haegeman, 2020) for the R 3.6–1 language and environment for statistical computing (R Core Team, 2019). A full DAISIE model with diversity dependence and no shifts includes five free parameters (colonization, cladogenesis, extinction, carrying capacity and anagenesis). An equivalent model with a single shift in all parameters includes 11 parameters: five parameters for the rates before the shift ($\lambda^c_1, \mu_1, K'_1, \gamma_1$ and λ^a_1), five parameters for the rates after the shift ($\lambda^c_2, \mu_2, K'_2, \gamma_2$ and λ^a_2) and a parameter specifying the time of the shift (t_{shift}).

2.3 | Colonization and diversification analyses

To test for the existence of a temporal shift in rates of community assembly in Lake Biwa fishes, we fitted a variety of DAISIE models. These included and excluded shifts, allowed for certain parameters to vary after the shift (or not) and included or excluded diversity dependence (i.e. switched on or switched off by fixing the carrying capacity parameter to infinity). This results in 80 different combinations ('candidate models'). We reduced this number to 40 candidate models (Table S2) by excluding shifts in cladogenetic rate. With a total of two cladogenetic speciation events within *Sarcocheilichthys* (Komiya, Fujita-Yanagibayashi, & Watanabe, 2014), there is too little information for two distinct cladogenetic rates. We estimated all rates, carrying capacities and the time of the shift by maximizing the likelihood of observing the given times of colonization and cladogenetic speciation. We fitted each candidate model using 10 random sets of starting conditions, to avoid being trapped in local likelihood maxima. Preliminary analyses showed that the time of the shift is particularly challenging to estimate. For the maximum likelihood search, we thus combined 10 random starting conditions with 10 initial shift times with a constant increment ranging from 0.1 Ma to the age of the insular system. Moreover, the estimation of the shift time was constrained to be more recent than the earliest colonization and speciation time derived from Biwa individuals (i.e. passing over 'MaxAge' status; Table S1) because 'Non_Endemic_MaxAge' and 'Endemic_MaxAge' lineages (which have no information on colonization or branching times) provide only information on species richness and endemism, which can cause inaccurate parameter estimates (Valente, Phillimore, & Etienne, 2018). We compared the support of the candidate models through Bayesian information criterion (BIC) weights. To account for potential equivocal support, we used the parameters of all models with weights greater than 0.05 to calculate the expected equilibrium diversity (Valente, Etienne, et al., 2017) and to stochastically simulate the diversity through time, which were then averaged by the respective BIC weights. In the Supporting Information, we evaluate the robustness of the model selection against uncertainties in (a) the number of colonist species ('mainland' pool in classic island biogeography), (b) the age of the oldest paleo-lake phase, (c) the estimated



colonization times and (d) in the species distribution (i.e. Lake Biwa itself vs. its drainage basin).

2.4 | Statistical power and precision

We evaluated whether the extended DAISIE model including rate-shifts correctly identifies a simulated shift (i.e. the statistical power) and quantified the discrepancy between simulated values and estimates by means of bootstrapping analysis. Using the 'DAISIE' R package, we simulated 5,000 datasets ('lakes') of phylogenetic colonization and speciation times with the rates estimated from the best-fit rate-constant and best-fit rate-shift models applied to Lake Biwa fishes. We then fitted the two models to each of the datasets and compared which was preferred using BIC, to examine the power of the method to correctly identify a shift when present, and to correctly reject a shift when it is absent. We also compared the estimated parameters for each dataset to those used to simulate, to assess the precision of the method.

Next, we aimed to identify the conditions under which DAISIE can robustly detect a shift in colonization rates (see Supporting Information). In brief, using the R package 'DAISIE' and assuming diversity independence, we simulated 5,000 datasets with an extant diversity similar to that of Lake Biwa fishes, allowing for a random increase in colonization rate between 3.9 and 0.1 Ma, and recorded all colonization, speciation and extinction times. We estimated the same parameters from the extant species with DAISIE (without diversity dependence) and from the full datasets (i.e. an idealized complete 'fossil record') with a multi-state Markov model using the R package 'msm' 1.6.6 (Jackson, 2011). Shifts not witnessed in a complete fossil record are unlikely to be recovered by DAISIE, which only includes branch lengths of extant species.

We then used structural equation modelling (SEM) and Bayes factor analysis to quantify how the difference in absolute fit between a shift and no-shift model (i.e. $\Delta\log$ -likelihood) and the relative error of the estimated shift time (i.e. the bias) depend on the simulated rates, the simulated magnitude of increase in colonization rate and the simulated shift time.

2.5 | Extending deterministic models of island biogeography

To demonstrate the consequence of source-sink dynamics and the geomorphology dependent colonization on diversity trajectories, we modified a deterministic simulation of the GDM (Borregaard et al., 2016) by (a) switching off the diversity dependence of the original implementation and (b) including a positive relationship of colonization with insular area and elevation (see also Cabral, Whittaker, et al., 2019). We applied two periods of island growth and high extinction rates (simulating source-sink dynamics) and conditioned on the extant fish diversity of Lake Biwa. We specified two scenarios where island expansion affects colonization rate or has no effect.

We provide the modified simulation code on <https://github.com/thauffe/simGDM>.

3 | RESULTS

3.1 | Colonization and diversification analyses

Assuming the largest colonist pool of 295 species and a lake age of 4 million years, a diversity-independent model including an increase in colonization rate for Lake Biwa fishes at 0.2 Ma (model M23) received the highest support (BIC weight = 0.36; Figure 2; Table S3). The simplest model M1, also diversity-independent but with no shifting parameters ranked second followed by model M25, which, in comparison to M23 included diversity dependence in both rates of colonization and cladogenesis (Figure 2a). Models featuring a shift 0.2 Ma always provided a better fit to the data than models with time-constant parameters across all scenarios of uncertainty in the limnological age of Lake Biwa, the size of the colonist pool, the estimated colonization times and the species distribution (Figure S1).

Averaging across simulated diversity trajectories of all models with a BIC weight >0.05 over the past 4 million years revealed a steady but declining build-up of fish species richness through time that closely approached the expected equilibrium diversity of 50 species before the shift in colonization rate 0.2 Ma (Figure 2b). After this shift, species richness increased to the levels observed today and the expected equilibrium diversity more than doubled. Therefore, contemporary diversity (70) is much below the theoretical equilibrium diversity. Projecting the future build-up of diversity suggests another 4 million years are needed to reach this elevated equilibrium diversity. Note that for all these models the theoretical equilibrium (both before and after the shift) is a source-sink type of equilibrium emerging from the fact that the rate of extinction exceeds the rate of in-situ cladogenesis and the model includes no (or only weak) diversity dependence.

The bootstrapping analysis using the estimated rates of the no-shift model and of our best-fit model featuring a shift in colonization rate (M1 and M23, respectively; Table S3) showed that the latter scenario is identifiable. Upon simulating constant colonization, the shift model was incorrectly selected in 3.4% of all 5,000 bootstrap replicates (i.e. low false-positive rate). In contrast, a simulated shift was correctly identified in 95.7% of all cases. In addition to the high power to identify the correct assembly scenario, all estimated values, except the underestimated colonization rate before the shift, showed little deviation from the generating ones (Figure S2).

3.2 | Limits to detecting rate shifts in DAISIE

The identified shift in colonization rate was very recent (0.2 Ma), and we thus evaluated with a second simulation approach whether we can identify an earlier shift with high statistical power. Using phylogenetic ages derived only from extant species (i.e. pruning all

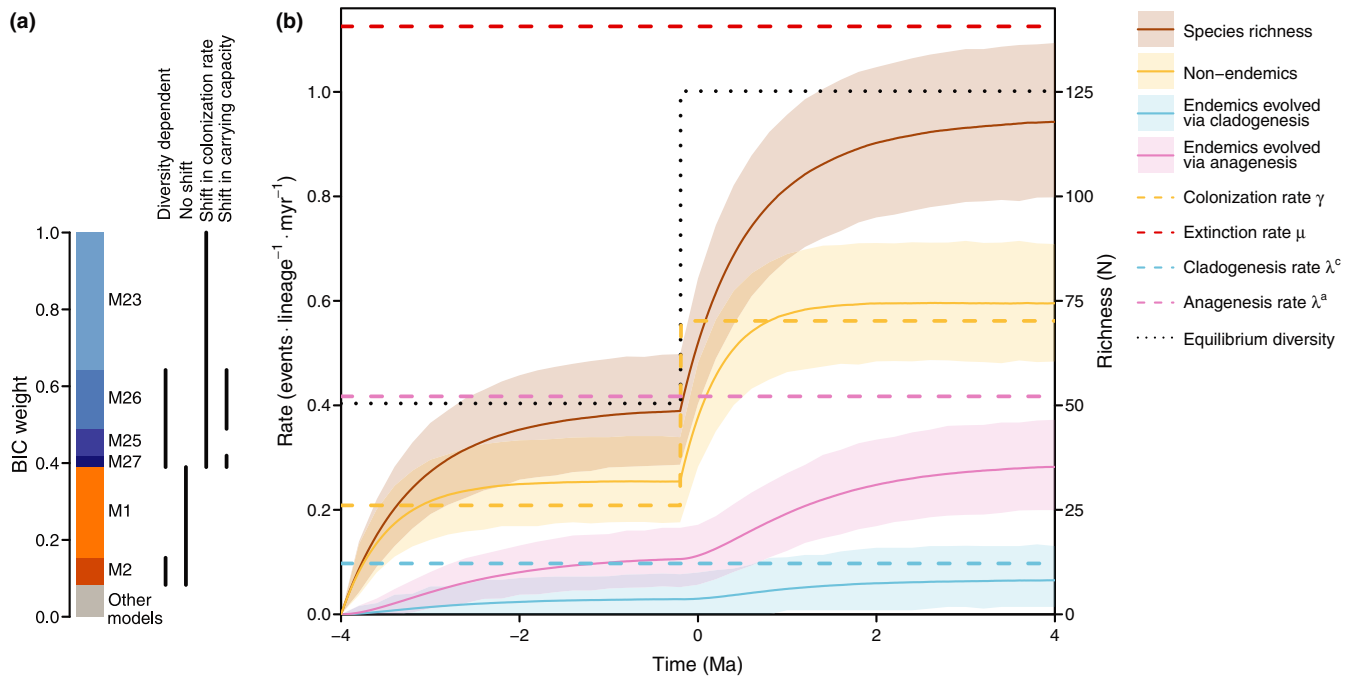


FIGURE 2 Diversity dynamics for the fishes of Lake Biwa. (a) Bayesian information criterion (BIC) weights displaying the relative support for diversity-dependent and diversity-independent models assuming a pool size of 295 species (explained in Table S2). Models with blue colours include an increase in colonization rate. Colour legend only shown for the six best models. (b) Via model support averaged rates, diversities and theoretical equilibrium plotted through the past 4 million years since the first limnological stages of Lake Biwa and extrapolated 4 million years into the future. Note that colonization rate is shown per species in the source pool, whereas the remaining rates are displayed per lake lineage [Colour figure can be viewed at wileyonlinelibrary.com]

extinct species from simulated datasets) and accepting a maximum bias in estimated shift time of 20%, DAISIE identified an increase in colonization rate in 24.5% of all simulated shifts between 3.9 and 0.1 Ma, which accounted for 41.8% of the shifts identified by the analyses using an idealized fossil record (including extinct species). The proportion of a correctly identified shift in colonization rate and its share in comparison to shifts identified by the fossil analyses increase with decreasing extinction rate and age of the generating shift (Figure S3).

The generalization of these trends through SEM and Bayes factor analysis allowed us to predict the limits to detect an increase in colonization rate by applying the inferred regression coefficients from the SEM to all combinations of colonization rates, extinction rate and shift time (Figure 3). This indicated that across replicated simulations it is only possible to simulate an early shift using high extinction rates and low colonization rates after the shift. An early shift decreases our ability to detect a shift (i.e. the likelihood improvement over a constant model) and increases the relative error of the estimated shift time. Given a source pool of 295 taxa, a diversity-independent model with a shift in a single parameter requires a fit of at least 7.6 log-likelihood units higher than a diversity-independent no-shift model to be supported using BIC. The proportion of parameter combinations exceeding such a likelihood improvement required to detect a true simulated scenario of increase in colonization rate decreases with an increase in extinction rate and with the age of the shift in colonization rate. With the extinction rate of 0.97 estimated

from the phylogenetic ages of the Lake Biwa fishes (Table S3), the earliest identifiable shift would be c. 1.5 Ma.

3.3 | Deterministic models of island biogeography

Our modified deterministic simulation of the GDM (Borregaard et al., 2016) resulted in a richness trajectory that quickly approached a source-sink equilibrium (Figure 4). With geomorphology-dependent colonization added, there is a slower rise in richness and a lower initial equilibrium diversity, which is exceeded during the second period of island expansion.

4 | DISCUSSION

To investigate the influence of geomorphological evolution on fish diversity of the ancient Lake Biwa and uncover the underlying mechanisms, we tested whether colonization and diversification rates changed through time and with diversity in this insular system. We detected an increase in colonization rate at 0.2 Ma, while models with no shifts, or with only shifts in parameters other than colonization, received lower support (Figure 2a). The colonization rate shift received a high bootstrap support of 96% and was robust to uncertainty in lake age, size of the colonist pool, estimated colonization times and species distribution (Figure S1). The shift was potentially

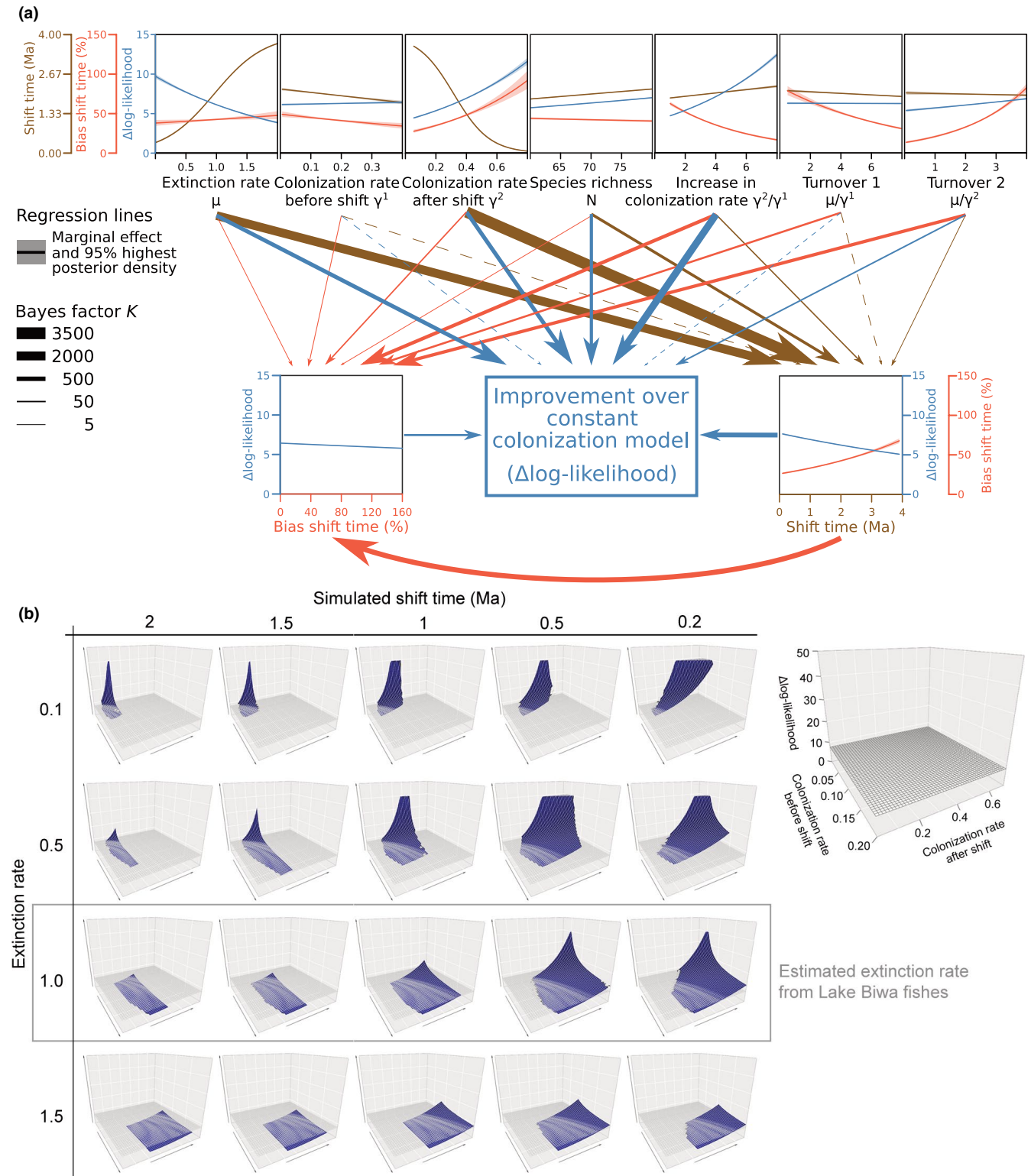


FIGURE 3 Power and limits to detecting a shift in colonization rate for the fishes of Lake Biwa. (a) Path diagram showing direct and indirect effects on which shift time in colonization rate is possible for a dataset like the Lake Biwa fishes (brown), the difference in the fit of a shift model over a no-shift scenario (i.e. $\Delta\log\text{-likelihood}$; blue) and the relative error of the estimated shift time (bias; red). Arrows are proportional to the decrease (solid) and increase (dashed), respectively, in fit of the path model upon omitting the path. (b) Improvement in likelihood for an increase in colonization rate over a model of constant rates predicted by the path modelling. All parameter combinations exceeding the horizontal plane indicate support in favour of the true simulated scenario, featuring an increase in colonization rate [Colour figure can be viewed at wileyonlinelibrary.com]

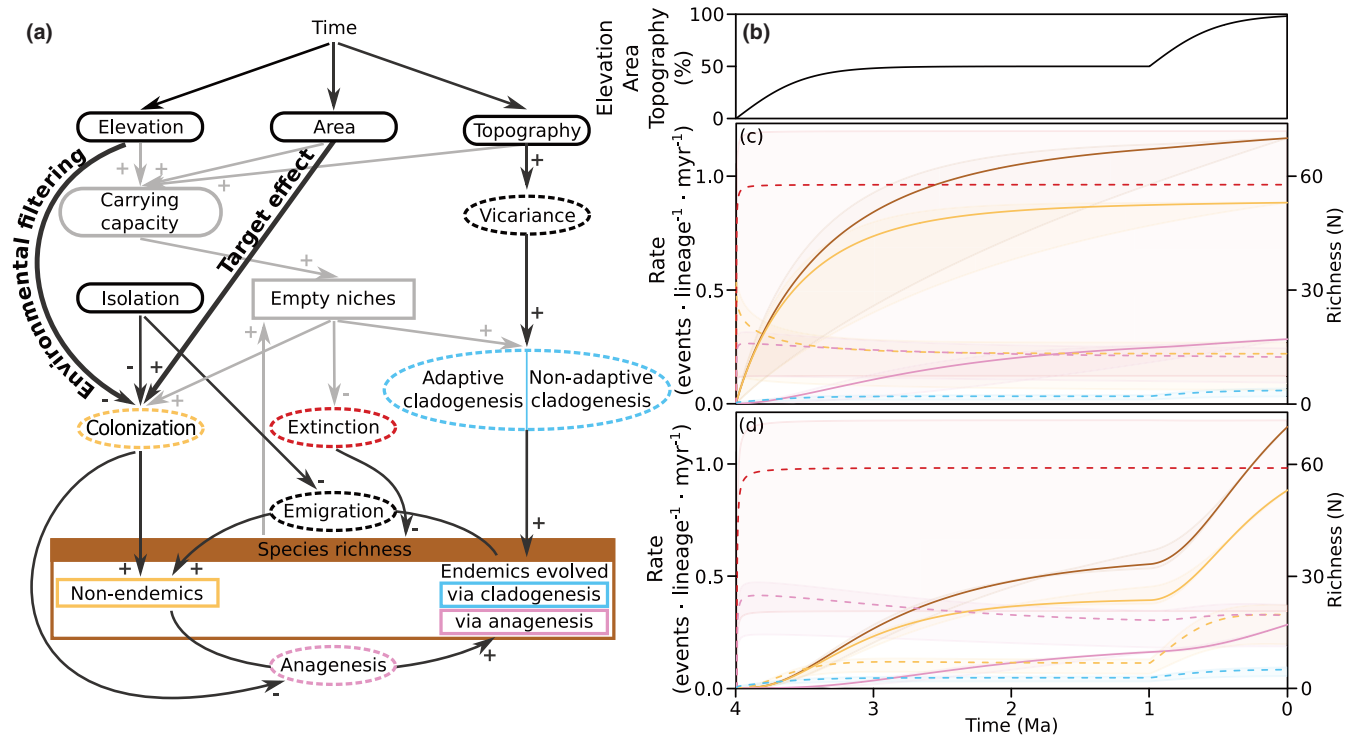


FIGURE 4 Target effect and environmental filtering integrated into the causal model of the general dynamic model of island biogeography and resulting diversity trajectories. (a) Redrawn Figure 3 of Borregaard et al. (2016) showing how island properties (ovals) shape species richness and endemism through biological processes (ellipses), which can be parameterized by a set of equations (arrows) that influence biological currencies (boxes). Light grey indicates components not needed for source-sink equilibrium dynamics. Richness and rate trajectories for the extant fish diversity of Lake Biwa according to (b) a hypothetical insular ontogeny and source-sink dynamics, (c) without or (d) with the positive influence of area and elevation on colonization rate. In contrast to the original causal model, speciation and extinction rates apply to the number of species of the insular ecosystem and colonization rate to the species of the source pool (as in Figure 3). Colours of the lines in (c) and (d) match those of (a) [Colour figure can be viewed at wileyonlinelibrary.com]

induced by an expansion of the lacustrine insular ecosystem, which altered the course of the diversity trajectory through time. Just prior to the shift, the estimated richness was close to the equilibrium diversity set by source-sink dynamics (diversity-independent). After the shift, the equilibrium diversity increased so that species richness is currently (still) far from this equilibrium. Our power analysis demonstrated that our new method to test for rate shifts based on phylogenetic data on extant species can infer half of the shifts in colonization rate that could be detected using a 'perfect' fossil record. Moreover, we could theoretically correctly detect a shift going as far back as c. 1.5 Ma (Figure 3), which covers the time-frame of major documented changes in the size of Lake Biwa.

4.1 | Shift in colonization rate: lake expansion or reduced isolation?

The relative support (i.e. BIC weight) for models including an increase in colonization rate over models without a shift was not very strong. However, the size of the colonist pool we used for the main analysis (295) is a maximum estimate where theoretically all Japanese diadromous and strictly freshwater fish could colonise Lake Biwa. The support for models featuring a shift in colonization

rate increased substantially with smaller colonist pools, which are more likely closer to the real value, due to the fish faunal subdivision of Japan (Watanabe, 2012). The mediocre support of shift models over simpler models we are focusing on is therefore conservative. Support also increased with the substitution of colonization times inferred for taxa with stable population sizes and when excluding strictly riverine and wetland taxa (Figure S1). However, our DAISIE models do not explicitly track geomorphological change as causal predictor of rates and therefore there could be other macroevolutionary mechanisms that could explain the temporal coincidence between the age of an identified shift and the documented geomorphological changes.

The increase in colonization rate, detected across different lake ages, colonist pool sizes, estimated colonization times and species distributions, follows the most significant period of tectonically induced increase in area and depth of Lake Biwa at 0.43 Ma (Okuda et al., 2014; Takemura, 1990) and the Penultimate Glacial Period where a sea-level decrease connected presently separated drainage basins (Dias et al., 2014). The former would suggest a more efficient target through a higher chance of colonization following an increase in area and/or a reduction of environmental filtering due to higher habitat heterogeneity upon lake expansion. Connecting drainage basins decreases the isolation of freshwater ecosystems and has



been shown to have homogenized freshwater fish communities via colonization (Dias et al., 2014). A decreasing isolation of Lake Biwa due to a larger drainage basin (Figure S4) should, in addition to its effect on colonization, decrease the rate of island-mainland differentiation ('anagenesis'; e.g. Valente et al., 2020). The corresponding model for this scenario (M8) showed an unexpected increase in rate of anagenesis and received low BIC support. In comparison, the lake expansion scenario M13 obtained higher BIC support and included the expected decrease in extinction rate and increase in colonization rate. This leads us to hypothesize that the increase in colonization of Lake Biwa was mainly driven by increased area/depth rather than decreased isolation, although the latter cannot be ruled out completely.

As with our finding of a time lag between lake expansion (0.43 Ma) and the estimated increase in colonization rate (0.2 Ma), the diversification rate and population sizes of endemic gastropods of Lake Biwa have also previously been shown to have experienced a delayed increase (Miura et al., 2019). Likewise, Tabata et al. (2016) found signatures of population growth 0.3–0.1 Ma for endemic and non-endemic fishes of Lake Biwa. While the exact reason for the time lag between the onset of lake expansion and the response of the fauna is unclear, species living at greater water depths seemed to have only recently immigrated or increased in their population size (Miura et al., 2019; Okuda et al., 2014).

Compared to the effect of area on speciation (Borregaard et al., 2016; Valente et al., 2014), the higher chance of colonization following an ecosystem expansion ('target effect') has received far less attention at evolutionary scales (Cabral, Whittaker, et al., 2019). The target effect has been widely discussed in insular studies of non-endemic richness (e.g. Lomolino, 1990; Si, Pimm, Russell, & Ding, 2014) and suggested as a driver of island species–area relationships (Santos, Field, & Ricklefs, 2016), but its potentially pivotal role in trajectories of diversity through time and island ontogeny has only recently been explored by simulation studies (Cabral, Whittaker, et al., 2019; Cabral, Wiegand, et al., 2019). The same simulation studies also suggested an increase in colonization rate due to increased chances of a match between the ecological niche of colonising taxa and the island's environment when habitat heterogeneity increases upon elevational growth. Our work thus provides unique empirical evidence for how changing ecosystem characteristics may drive rates of species gain through the effect of area and depth on colonization.

4.2 | Shifting equilibria

The richness trajectory derived from the estimated rates and averaged across models approaches equilibrium diversity prior to Lake Biwa's expansion (Figure 2b). This differs from the attained long-term equilibrium dynamics previously found on some oceanic islands (Rabosky & Glor, 2010; Valente, Illera, et al., 2017). However, insular ecosystems with non-equilibrium dynamics are also well known (Jönsson et al., 2012; Schoener, 2010; Valente, Etienne, et al.,

2017) and debates revolve around whether a carrying capacity exists (Harmon & Harrison, 2015), whether it varies with time and area (Marshall & Quental, 2016) and whether equilibrium dynamics may ever be attained at all on islands (Warren et al., 2015; Whittaker et al., 2008). Whereas the global fossil record suggests changes in carrying capacity over time (Bush, Hunt, & Bambach, 2016), molecular phylogenies have rarely demonstrated such a change (but see Matos-Maraví et al., 2014). Using phylogenetic estimates of colonization and speciation times, our study supports the notion that ecosystem ontogeny shapes the level of equilibrium diversity. Because extinction rates always exceeded the rate of in-situ cladogenesis, the quasi-equilibrium we found at 0.2 Ma and its model-averaged increase afterwards appear to be the result of source-sink dynamics and, according to its low relative support (i.e. BIC weight), less likely a consequence of diversity dependence induced by ecological limits. Moreover, the diversity dependence parameter in the model decreased rather than increased. For our data, we could therefore not detect the increase in ecological limits predicted by the GDM. However, our DAISIE implementation assumes clade-specific diversity dependence where diversity dependence only occurs within the clade established by each colonising mainland species. Current methods do not yet allow for assessing island-wide diversity dependence where all species on the island affect each other's rates of colonization and cladogenesis.

In insular ecosystems with source-sink dynamics, or with a mild diversity-dependent feedback, the actual level of the equilibrium diversity depends on the colonization rate (and the rate of in-situ cladogenesis and extinction). Diversity-dependent or -independent models consistently suggested a rise in colonization rate at 0.2 Ma, which caused a substantial elevation of the expected equilibrium diversity. Given the estimated rates following the shift, species richness will only reach this level after 4 Ma, as suggested by our stochastic simulations of future diversity (Figure 2).

The mechanism underlying this inferred diversity trajectory can be elucidated by the deterministic simulations of a causal model of island biogeography (Figure 4), which we modified to include diversity-independent equilibria and an area/depth effect on colonization. The emerging diversity dynamics after adding these mechanisms (Figure 4d) resembled the estimated diversity trajectory for the fishes of Lake Biwa (Figure 2). Moreover, a high extinction rate and lack of ecological limits are key components to generate this diversity trajectory. This mirrors the parameters of the best-fit Lake Biwa fish model, suggesting similar mechanisms to operate.

4.3 | Model performance, limitations and future directions

There are some limits to the circumstances under which we can find support for an increase in colonization rate. Our extensive simulations and maximum likelihood optimizations revealed that the chances thereof decreased with a lower increase in colonization rate, higher extinction and a higher age of the shift (Figure 3a),

as expected. With the extinction rate estimated from the phylogenetic ages of the Lake Biwa fishes, the earliest identifiable shift would be 1.5 Ma (Figure 3b). This suggests that we could theoretically trace the signature of three major stages of lake evolution (i.e. the disappearance of Lake Gamo 1.8 Ma, the formation of Lake Katata 1.0 Ma and the expansion of modern Lake Biwa 0.4 Ma; Takemura, 1990). It also implies that a potential imprint of earlier limnological changes on the fish assemblage is beyond what we can infer with our phylogenetic age estimates because extinction removes such a signal. A consequence of this signal removal is a positive correlation of extinction with colonization rate before the shift, and explains why the latter parameter showed a lower estimation accuracy compared to the other parameters (Figure S2). The same correlation has been noted before in DAISIE, but did not impair the selection of the correct model (Valente et al., 2015). The high estimated extinction rate seems to be in agreement with the fossil record of Lake Biwa, showing drastic changes of its fish community composition through time (Nakajima, 2012). Given an average richness of approximately 50 taxa over the past 4 Ma (Figure 2), our extinction rate indicates that almost 200 taxa became extinct in Lake Biwa in this period, thus reflecting the dynamics of the fossil record.

Previous studies highlighted the reservoir function of Lake Biwa, facilitating a back-colonization upon extirpation in the rest of Japan or the harbouring of 'relict species' (Okuda et al., 2014; Tabata et al., 2016). While DAISIE does not include an emigration rate out of the insular system, our results are not affected by this because the initial colonization time remains unaffected and the rate of anagenesis includes the formation of 'relict species'.

A limitation of our approach is that we only included a single shift, but island and lake ontogenies suggest multiple shifts. These are possible to implement but would require extensive simulations to evaluate what magnitudes of parameter shifts are needed for robust estimation. The continuous geological evolution of an insular system may only be poorly approximated by modelled shifts in evolutionary rates and carrying capacity, and may be better described by continuous time-varying diversification models (Rabosky & Glor, 2010).

5 | CONCLUSIONS

Our extension of the DAISIE framework to allow for shifts in rates of insular biota assembly revealed that the fish species richness of Lake Biwa was close to a source-sink equilibrium diversity until approximately 0.2 Ma. The increase in colonization rate upon lake expansion caused a shift towards a much larger fish diversity, and thus the system is currently far from its theoretical equilibrium. This demonstrates that the geological evolution of an insular ecosystem influences its biodiversity. The revealed area and depth-dependent colonization supports the integration of the target effect and environmental filtering into causal models of island biogeography over evolutionary time periods.

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CONFLICT OF INTEREST

LV is an associate editor of the Journal of Biogeography.

DATA AVAILABILITY STATEMENT

All data are sourced from literature and available as Supplementary Information and within the R package 'DAISIE'.

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BIOSKETCH

Torsten Hauffe uses geological and biological data to explore past and present biodiversity dynamics and their underlying drivers. He is specifically interested in understanding processes of community assembly over ecological and evolutionary time-scales. His work is primarily focused on freshwater taxa.

Author contributions: DD and TH conceived the research idea; DD compiled the phylogenetic data; TH wrote the first draft; RSE refined the modified DAISIE analysis; LV and TH performed the analyses and all authors discussed the results and contributed to the writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX 1

DATA SOURCES

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